

# Dynamical mean-field theory of spiking neuron ensembles: response to a single spike with independent noises <sup>\*</sup>

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## Abstract

Dynamics of an ensemble of  $N$ -unit FitzHugh-Nagumo (FN) neurons subject to white noises has been studied by using a semi-analytical dynamical mean-field (DMF) theory in which the original  $2N$ -dimensional *stochastic* differential equations are replaced by 8-dimensional *deterministic* differential equations expressed in terms of moments of local and global variables. Our DMF theory, which assumes weak noises and the Gaussian distribution of state variables, goes beyond weak couplings among constituent neurons. By using the expression for the firing probability due to an applied single spike, we have discussed effects of noises, synaptic couplings and the size of the ensemble on the spike timing precision, which is shown to be improved by increasing the size of the neuron ensemble, even when there are no couplings among neurons. When the coupling is introduced, neurons in ensembles respond to an input spike with a partial synchronization. DMF theory is extended to a large cluster which can be divided into multiple sub-clusters according to their functions. A model calculation has shown that when the noise intensity is moderate, the spike propagation with a fairly precise timing is possible among noisy sub-clusters with feed-forward couplings, as in the synfire chain. Results calculated by our DMF theory are nicely compared to those obtained by direct simulations. A comparison of DMF theory with the conventional moment method is also discussed.

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## I. INTRODUCTION

It has been controversial how neurons communicate information by firings or spikes [1]-[6]. Much of debates on the nature of the neural code has been mainly focused on the two issues. The first issue is whether information is encoded in the average firing rate of neurons (*rate code*) or in the precise firing times (*temporal code*). Adrian [7] first noted the relationship between the neural firing rate and the stimulus intensity, which forms the basis of the rate code. Actually firing activities of motor and sensory neurons are reported to vary in response to applied stimuli. In recent years, however, an alternative temporal code has been proposed in which detailed spike timings are assumed to play an important role in information transmission: information is encoded in interspike intervals or in relative timings between firing times of spikes [8]- [10]. Indeed, experimental evidences have accumulated in the last several years, indicating a use of the temporal coding in neural systems [11]-[15]. Human visual systems, for example, have shown to classify patterns within 250 ms despite the fact that at least ten synaptic stages are involved from retina to the temporal brain [15]. The transmission times between two successive stages of synaptic transmission are suggested to be no more than 10 ms on the average. This period is too short to allow rates to be determined accurately.

The second issue is whether information is encoded in the activity of a single (or very few) neuron or that of a large number of neurons (*population* or *ensemble code*). The population rate-code model assumes that information is coded in the relative firing rates of ensemble neurons, and has been adopted in the most of the theoretical analysis [16]. On the contrary, in the population temporal-code model, it is assumed that relative timings between spikes in ensemble neurons may be used as an encoding mechanism for perceptual processing [17]- [19]. A number of experimental data supporting this code have been reported in recent years [20]- [21]. For example, data has demonstrated that temporally coordinated spikes can systematically signal sensory object feature, even in the absence of changes in firing rate of the spikes [22].

It is well known that neurons in brains are subject to various kinds of noises, which can alter the response of neurons in various ways. Although firings of a single neocortical neuron in *vitro* are precise and reliable, those in *vivo* are quite unreliable [23]. This is due to noisy environment in *vivo*, which makes the reliability of neurons firings worse. The strong criticism against the temporal code is that spikes are vulnerable to noise while the rate code performs robustly in the presence of noise but with limited information capacity. It has been shown, however, that the response of neurons is improved by background noises against our conventional wisdom. The typical example is the stochastic resonance (SR), in which weak noises enhance the transmission of subthreshold signals (for review see Refs. [24] [25]). It has been shown that noise of appropriate magnitude linearizes the response of neurons, which leads to SR and maximizes input-output correlation, transformation and coherence (for review see Ref. [26]). Recently, it has been demonstrated that noises can enhance the firing-time reliability of neurons stimulated by weak periodic and aperiodic inputs [27]- [29]. We may expect that a population of neuron ensembles plays important roles in the response of neurons subject to noises. Actually SR in HH neuron ensembles has first demonstrated for a single input by Pei, Wilkens and Moss [30]. Subsequently this pooling effect has been supported for aperiodic [31] [32] and periodic (analog) signals [33] and for spike-train inputs

[34] [35]. Quite recently, SR for a transient spike signal in large-scale HH neuron ensembles has been studied by using the wavelet analysis [34]. It may be possible that the firing-time precision is also improved by increasing the size of neuron ensembles.

A small patch of cortex may contain thousands of similar neurons, each connecting with hundreds or thousands of other neurons in that same patch or in other patches. The underlying dynamics of individual neurons includes a variety of voltage dependent ionic channels which can be described by Hodgkin-Huxley-type differential equations. Computational neuroscientists have so far tried to gain understanding of the properties of neuron ensembles with the use of two approaches: direct simulations and mean-field (MF) theories. Simulations have been made for large-scale networks mostly consisting of integrate-and-fire (IF) neurons. Since the time to simulate networks by conventional methods grows as  $N^2$  with  $N$ , the size of the network [36], it is rather difficult to simulate realistic neuron clusters, in spite of recent computer development. In MF theories [37]- [40], dynamics of globally coupled large-scale networks is described by a flow of phases or the population activity, which determines the fraction of the firing rate of neurons. The stability condition for synchronous and asynchronous states of neuron clusters has been investigated. Quite recently, the population density method has been developed as a tool modeling for large-scale neuronal clusters [41]- [42]. In these MF approaches the macroscopic variable of interest is the firing rate, following the *rate-code* hypothesis. However, only little MF approaches have so far proposed based on the temporal-code hypothesis [39] [40].

The purpose of the present study is to construct a dynamical mean-field (DMF) theory based on the temporal code hypothesis, generalizing the method previously proposed by Rodriguez and Tuckwell (RT) [43]- [46]. In the RT theory, the dynamics of the membrane potential of a neuron subject to white noises is studied by replacing *stochastic* differential equations (DEs) by *deterministic* DEs described by moments of state variables. RT's general theory has first applied to a single FitzHugh-Nagumo (FN) neuron [43] [44] and then a Hodgkin-Huxley (HH) neuron [45] [46]. In the case of a single FN neuron, for example, two stochastic DEs are replaced by five deterministic DEs, for which an improvement to the RT theory has been recently proposed [47]. When the RT theory is applied to a  $N$ -unit FN neuron network,  $2N$  stochastic DEs are replaced by  $N_{eq} = N(2N + 3)$  deterministic DEs [43] [46]. For example, in the case of  $N = 100$ , we get  $N_{eq} = 20300$ , which is too large to perform calculations for neuron ensembles. In their subsequent paper [45], the result of ensemble neurons is transplanted to the Fokker-Planck (FP) equation for the transition probability density, which is a partial differential equation with  $2N+1$  independent variables. Solving such a FP equation is a hard computational task. We will present in this paper, an alternative MF theory for  $N$  FN neuron ensembles, replacing original  $2N$  stochastic DEs by *eight* deterministic DEs which are expressed in terms of means, variances and covariances of *local* and *global* state variables.

There are several nonlinear models which have been used for a study of neuron activities. Among them we employ here the FN model [48] [49] because it is relatively simple and amenable to analysis although the FN model does not have as firm an empirical basis as conductance-based model like the HH model. The property of the FN model has been intensively investigated. In recent years, SR of a single FN neuron [50]- [52] and FN neuron ensembles [31] [32] [53] [54] have been studied.

The paper is organized as follows: In Sec. II, we have developed a DMF theory for  $N$

FN neuron ensembles, expanding the original stochastic DEs in terms of deviations from means to get variances and covariances of local and global variables. We compare our DMF theory with conventional RT's moment method [43], showing that the former may be derived from the latter. Some calculated results are reported of the response of ensemble neurons to a single spike with white noises. It will be shown that the spike firing precision is improved by increasing the ensemble size and the synaptic couplings, as expected. In Sec. III. DMF theory is extended to a large cluster consisting of multiple sub-clusters and model calculations are reported. The final Sec. IV is devoted to conclusions and discussions.

## II. NEURON ENSEMBLES

### A. DMF approximation

We assume a neuron ensemble consisting of  $N$ -unit FN neurons. Dynamics of a single FN neuron  $i$  in a given ensemble is described by the nonlinear DEs given by

$$\frac{dx_i(t)}{dt} = F[x_i(t)] - cy_i(t) + I_i^{(c)}(t) + I^{(e)}(t) + \xi_i(t), \quad (1)$$

$$\frac{dy_i(t)}{dt} = bx_i(t) - dy_i(t) + e, \quad (i = 1 - N) \quad (2)$$

where  $F[x(t)] = k x(t) [x(t) - a] [1 - x(t)]$ ,  $k = 0.5$ ,  $a = 0.1$ ,  $b = 0.015$ ,  $c = 1.0$ ,  $d = 0.003$  and  $e = 0$  [43] [44],  $x_i$  and  $y_i$  denote the fast (voltage) variable and slow (recovery) variable, respectively, and  $\xi_i(t)$  is the independent Gaussian white noise with  $\langle \xi_i(t) \rangle = 0$  and  $\langle \xi_i(t) \xi_j(t') \rangle = \beta_i^2 \delta_{ij} \delta(t - t')$ , the bracket  $\langle \cdot \rangle$  denoting the average over stochastic random variables [55]. In Eq. (1),  $I_i^{(c)}(t)$  denotes the coupling term given by

$$I_i^{(c)}(t) = \frac{w}{N} \sum_{j(\neq i)} G(x_j(t)), \quad (3)$$

where  $w$  stands for the coupling strength and  $G(x) = 1/[1 + \exp[-(x - \theta)/\alpha]]$  is the sigmoid function with the threshold  $\theta$  and the width  $\alpha$ . The self-coupling terms are excluded in Eq. (3), where we have adopted the normalization factor to be  $N^{-1}$  instead of  $(N - 1)^{-1}$  for a later study of the  $N = 1$  limit.  $I^{(e)}(t)$  expresses an external, single spike input applied to all neurons, given by

$$I^{(e)}(t) = A \Theta(t - t_{in}) \Theta(t_{in} + T_w - t), \quad (4)$$

where  $\Theta(x) = 1$  for  $x > 0$  and 0 otherwise,  $A$  stands for the magnitude,  $t_{in}$  the input time and  $T_w$  the width.

After RT [43] [44], we will express these nonlinear DEs by moments of variables. First we define the global variables for the ensemble by

$$X(t) = (1/N) \sum_i x_i(t), \quad (5)$$

$$Y(t) = (1/N) \sum_i y_i(t), \quad (6)$$

and their averages by

$$\mu_1(t) = \langle X(t) \rangle, \quad (7)$$

$$\mu_2(t) = \langle Y(t) \rangle. \quad (8)$$

Next we express the differential equations given by Eqs. (1) and (2) in terms of the deviations from their averages defined by

$$\delta x_i(t) = x_i(t) - \mu_1(t), \quad (9)$$

$$\delta y_i(t) = y_i(t) - \mu_2(t), \quad (10)$$

to get (the argument  $t$  is hereafter neglected)

$$\begin{aligned} \frac{dx_i}{dt} = & F(\mu_1) + F'(\mu_1)\delta x_i + \frac{1}{2}F^{(2)}(\mu_1)\delta x_i^2 + \frac{1}{6}F^{(3)}(\mu_1)\delta x_i^3 \\ & - c\mu_2 - c\delta y_i + I_i^{(c)} + I_i^{(e)} + \xi_i, \end{aligned} \quad (11)$$

$$\frac{dy_i}{dt} = b\mu_1 - d\mu_2 + b\delta x_i - d\delta y_i + e, \quad (12)$$

with

$$\begin{aligned} I_i^{(c)} = & w\left\{\left(1 - \frac{1}{N}\right)G(\mu_1) \right. \\ & \left. + \frac{1}{N} \sum_{j(\neq i)} [G'(\mu_1)\delta x_j + \frac{1}{2}G^{(2)}(\mu_1)\delta x_j^2 + \frac{1}{6}G^{(3)}(\mu_1)\delta x_j^3]\right\}. \end{aligned} \quad (13)$$

We define the variances and covariances between local variables, given by

$$\gamma_{1,1} = \frac{1}{N} \sum_i \langle \delta x_i^2 \rangle, \quad (14)$$

$$\gamma_{2,2} = \frac{1}{N} \sum_i \langle \delta y_i^2 \rangle, \quad (15)$$

$$\gamma_{1,2} = \frac{1}{N} \sum_i \langle \delta x_i \delta y_i \rangle, \quad (16)$$

and those between global variables, given by

$$\rho_{1,1} = \langle \delta X^2 \rangle, \quad (17)$$

$$\rho_{2,2} = \langle \delta Y^2 \rangle, \quad (18)$$

$$\rho_{1,2} = \langle \delta X \delta Y \rangle, \quad (19)$$

where  $\delta X = X(t) - \mu_1(t)$  and  $\delta Y = Y(t) - \mu_2(t)$ . It is noted that  $\gamma_{\kappa,\lambda}$  expresses the spatial average of fluctuations in local variables of  $x_i$  and  $y_i$  while  $\rho_{\kappa,\lambda}$  denotes fluctuations in global variables of  $X$  and  $Y$ . We assume that (1) the noise intensity  $\beta$  is weak and (2) the distribution of state variables take Gaussian form. The first assumption allows us to expand the quantities in a power series of fluctuation moments around means. As for the second assumption, numerical simulations have shown that for weak noises, the distribution of  $x(t)$

of the membrane potential of a single FN neuron nearly obeys the Gaussian distribution, although for strong noises, the distribution of  $x(t)$  deviates from the Gaussian, taking a bimodal form (see Fig. 8 of Ref. [44] and Fig. 3 of Ref. [47]). Similar behavior of the membrane-potential distribution has been reported in a HH neuron model [33] [28]. When adopting the Gaussian assumption, we may express the average of fluctuations in terms of the first and second moments only. It is noted that we impose no conditions on the coupling strength. After some manipulations, we get DEs for means, variances and covariances, given by (for details see Appendix A):

$$\frac{d\mu_1}{dt} = f_0 + f_2\gamma_{1,1} - c\mu_2 + w \left(1 - \frac{1}{N}\right) U_0 + I^{(e)}(t), \quad (20)$$

$$\frac{d\mu_2}{dt} = b\mu_1 - d\mu_2 + e, \quad (21)$$

$$\frac{d\gamma_{1,1}}{dt} = 2[(f_1 + 3f_3\gamma_{1,1})\gamma_{1,1} - c\gamma_{1,2}] + 2w(\rho_{1,1} - \frac{\gamma_{1,1}}{N}) U_1 + \beta^2, \quad (22)$$

$$\frac{d\gamma_{2,2}}{dt} = 2(b\gamma_{1,2} - d\gamma_{2,2}), \quad (23)$$

$$\frac{d\gamma_{1,2}}{dt} = b\gamma_{1,1} + (f_1 + 3f_3\gamma_{1,1} - d)\gamma_{1,2} - c\gamma_{2,2} + w \left(\rho_{1,2} - \frac{\gamma_{1,2}}{N}\right) U_1, \quad (24)$$

$$\frac{d\rho_{1,1}}{dt} = 2[(f_1 + 3f_3\gamma_{1,1})\rho_{1,1} - c\rho_{1,2}] + 2w \left(1 - \frac{1}{N}\right) \rho_{1,1} U_1 + \frac{\beta^2}{N}, \quad (25)$$

$$\frac{d\rho_{2,2}}{dt} = 2(b\rho_{1,2} - d\rho_{2,2}), \quad (26)$$

$$\frac{d\rho_{1,2}}{dt} = b\rho_{1,1} + (f_1 + 3f_3\gamma_{1,1} - d)\rho_{1,2} - c\rho_{2,2} + w \left(1 - \frac{1}{N}\right) \rho_{1,2} U_1, \quad (27)$$

with

$$U_0 = g_o + g_2\gamma_{1,1}, \quad (28)$$

$$U_1 = g_1 + 3g_3\gamma_{1,1}, \quad (29)$$

$$f_\ell = (1/\ell!)F^{(\ell)}(\mu_1), \quad (30)$$

$$g_\ell = (1/\ell!)G^{(\ell)}(\mu_1). \quad (31)$$

where  $\beta^2 = (1/N) \sum_i \beta_i^2$ .

The original  $2N$ -dimensional *stochastic* differential equations given by Eqs. (1) and (2) are transformed to eight-dimensional *deterministic* differential equations, which show much variety depending on model parameters such as the strength of white noise ( $\beta$ ), couplings ( $w$ ) and the size of cluster ( $N$ ).

## B. Derivation of DMF theory from RT's moment method

Before discussing the property of our DMF theory, we will show that it can be derived from RT's moment method [43]. In the case of a single FN neuron ( $N = 1$ ), DMF theory agrees with the RT theory as shown in appendix B, where some limiting cases of Eqs. (20)-(27) are examined. In the case of FN neuron ensemble ( $N \geq 2$ ), the RT theory defines means of variables of  $x_i$  and  $y_i$  for the neuron  $i$  given by

$$m_1^i = \langle x_i \rangle, \quad (32)$$

$$m_2^i = \langle y_i \rangle, \quad (33)$$

and calculate variances and covariances between *local* variables as given by

$$C_{1,1}^{i,j} = \langle \Delta x_i \Delta x_j \rangle, \quad (34)$$

$$C_{2,2}^{i,j} = \langle \Delta y_i \Delta y_j \rangle, \quad (35)$$

$$C_{1,2}^{i,j} = \langle \Delta x_i \Delta y_j \rangle, \quad (36)$$

where  $\Delta x_i = x_i - m_1^i$  and  $\Delta y_i = y_i - m_2^i$ . Variances are given by setting  $i = j$  in Eqs. (34)-(35). Adopting the same assumptions as our DMF theory: (1) weak noises and (2) the Gaussian distribution for state variables, we get DEs for these moments given by (for details see Appendix A)

$$\frac{dm_1^i}{dt} = f_0^i + f_2^i C_{1,1}^{i,i} - c m_2^i + \frac{w}{N} \sum_{j(\neq i)} [g_o^j + g_2^j C_{1,1}^{j,j}] + I^{(e)}, \quad (37)$$

$$\frac{dm_2^i}{dt} = b m_1^i - d m_2^i + e, \quad (38)$$

$$\begin{aligned} \frac{dC_{1,1}^{i,j}}{dt} = & (f_1^i + 3f_3^i C_{1,1}^{i,i} + f_1^j + 3f_3^j C_{1,1}^{j,j}) C_{1,1}^{i,j} - c(C_{1,2}^{i,j} + C_{2,1}^{i,j}) + \beta^2 \delta_{ij} \\ & + \frac{w}{N} \left[ \sum_{k(\neq i)} (g_1^k + 3g_3^k C_{1,1}^{k,k}) C_{1,1}^{j,k} + \sum_{k(\neq j)} (g_1^k + 3g_3^k C_{1,1}^{k,k}) C_{1,1}^{i,k} \right], \end{aligned} \quad (39)$$

$$\frac{dC_{2,2}^{i,j}}{dt} = b(C_{1,2}^{i,j} + C_{2,1}^{i,j}) - 2dC_{2,2}^{i,j}, \quad (40)$$

$$\begin{aligned} \frac{dC_{1,2}^{i,j}}{dt} = & bC_{1,1}^{i,j} + (f_1^i + 3f_3^i C_{1,1}^{i,i} - d) C_{1,2}^{i,j} - cC_{2,2}^{i,j} \\ & + \frac{w}{N} \sum_{k(\neq i)} (g_1^k + 3g_3^k C_{1,1}^{k,k}) C_{2,1}^{j,k}, \end{aligned} \quad (i, j = 1 \text{ to } N) \quad (41)$$

where

$$f_\ell^i = (1/\ell!) F^{(\ell)}(m_1^i), \quad (42)$$

$$g_\ell^i = (1/\ell!) G^{(\ell)}(m_1^i). \quad (43)$$

Now we derive DMF theory from RT's moment method. We adopt the approximation given by

$$m_1^i = \mu_1, \quad (44)$$

which yields  $f_\ell^i = f_\ell$  and  $g_\ell^i = g_\ell$  [Eqs. (28), (29), (42) and (43)], and the approximation given by

$$\begin{aligned} f_3 C_{1,1}^{i,i} & \simeq f_3 \gamma_{1,1}, \\ g_3 C_{1,1}^{k,k} & \simeq g_3 \gamma_{1,1}. \end{aligned} \quad (45)$$

in Eqs. (39) and (40). We realize that quantities of  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda}$  [Eqs. (5)-(8) and (14)-(19)] adopted in DMF theory are expressed in terms of  $m_\kappa^i$  and  $C_{\kappa,\lambda}^{i,j}$  [Eqs. (32)-(36)] in the RT theory as follows:

$$\mu_\kappa = \frac{1}{N} \sum_i m_\kappa^i, \quad (46)$$

$$\gamma_{\kappa,\lambda} = \frac{1}{N} \sum_i C_{\kappa,\lambda}^{i,i}, \quad (47)$$

$$\rho_{\kappa,\lambda} = \frac{1}{N^2} \sum_i \sum_j C_{\kappa,\lambda}^{i,j}. \quad (\kappa, \lambda = 1, 2) \quad (48)$$

Then, we may obtain, from Eqs. (37)-(41), (44)-(48), alternative DEs for  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda}$  which are again given by Eqs. (20)-(27). This implies that DMF theory may be derived from RT's moment method if we adopt the assumptions given by Eq. (44) and (45) [56].

Taking into the symmetry relations:  $C_{\kappa,\lambda}^{i,j} = C_{\kappa,\lambda}^{j,i}$ , we get the number of DEs to be  $N_{eq} = 2N + N(2N + 1) = N(2N + 3)$  in the RT theory [Eqs. (37)-(41)] while  $N_{eq} = 8$  in our DMF theory [Eq. (20)-(27)] ( $N_{eq} = 2NN_{tr}$  in direct simulations where  $N_{tr}$  denotes the number of trials). In the case of  $N = 100$ , for example, we get  $N_{eq} = 20300$  in the RT method, which is much larger than  $N_{eq} = 8$  in DMF theory. Our DMF theory successfully reduces the number of DEs, by taking account  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda}$  for *global* variables as well as *local* variables instead of  $m_\kappa^i$  and  $C_{\kappa,\lambda}^{i,j}$  for local variables. Although our DMF theory neglects spatial fluctuations in state variables, it has advantages of a tractable small number of DEs and clear semi-analytical nature, from which some qualitative results may be deduced without numerical calculations, as will be shown shortly [*e.g.* Eq. (52)]. When couplings have the spatial dependence as  $w \rightarrow w_{ij}$  in Eq. (3), we have to rely on Eqs. (37)-(41) in the moment method.

### C. Property of DMF theory

In this subsection, we will discuss the property of our DMF theory. It is possible to regard DMF theory as the single-site mean-field theory. Let us assume a configuration in which a *single* neuron  $i$  is embedded in an effective *medium* whose effect is realized by a given neuron  $i$  as its *effective* external input through the coupling  $w$ . We replace quantities of  $m_\kappa^k$ ,  $C_{\kappa,\lambda}^{k,k}$  and  $(1/N) \sum_{k(\neq \ell)} C_{\kappa,\lambda}^{\ell,k}$  in coupling terms of Eqs. (37)-(41) by effective quantities of  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda} - (1/N)\gamma_{\kappa,\lambda}$ , respectively. Then, in order to determine these quantities just introduced, we impose the *single-site* mean-field conditions given by [see Eqs. (46)-(48)]

$$\mu_\kappa = m_\kappa^i, \quad (49)$$

$$\gamma_{\kappa,\lambda} = C_{\kappa,\lambda}^{i,i}, \quad (50)$$

$$\rho_{\kappa,\lambda} - \frac{1}{N} \gamma_{\kappa,\lambda} = \frac{1}{N} \sum_{j(\neq i)} C_{\kappa,\lambda}^{i,j}. \quad (51)$$

Note that Eqs. (49)-(51) are assumed to hold independently of  $i$  and that  $m_\kappa^i$  and  $C_{\kappa,\lambda}^{i,j}$  in their righthand sides are functions of  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda}$ . Conditions given by Eqs. (49)-(51) yield the self-consistent DEs for  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda}$  which are again given by Eqs. (20)-(27). The



single-site approximation given by Eq. (49)-(51), which assumes that the quantities averaged at a given site are the same as those of the effective medium, is common in mean-field theories such as the Weiss theory for magnetism [57] and the coherent-potential approximation for random alloys [58].

We should note that the noise contribution is  $\beta^2$  in Eq. (22) while that is  $\beta^2/N$  in Eq. (25). It is easy to see that in the case of no couplings, we get

$$\rho_{\kappa,\lambda} = \frac{\gamma_{\kappa,\lambda}}{N}, \quad (\text{for } w = 0) \quad (52)$$

which agrees with the *central-limit theorem*. On the other hand, in the case of  $\beta = 0$  and  $w \neq 0$ , we get  $\rho_{\kappa,\lambda} = \gamma_{\kappa,\lambda}$ . Thus the ratio:  $\rho_{\kappa,\lambda}/\gamma_{\kappa,\lambda}$  changes as model parameters are changed. We will show that these changes in  $\rho_{\kappa,\lambda}$  and  $\gamma_{\kappa,\lambda}$  reflect on the firing time distribution and the degree of synchronous firings in neurons ensembles.

### Firing-Time Distribution

The ( $n$ th) firing time of a given neuron  $i$  in the ensemble is defined as the time when  $x_i(t)$  crosses the threshold  $\theta$  from below:

$$t_{oin} = \{t \mid x_i(t) = \theta; \dot{x}_i > 0; t \geq t_{oin-1} + \tau_r\}, \quad (53)$$

where  $\tau_r$  denotes the refractory period introduced so as to avoid multiple firings in a short period arising from fluctuations in voltage variables around the threshold. We get the distribution for the membrane potential variable  $x_i$  given by (for details see Appendix C)

$$P(x_i) \simeq \left(\frac{1}{\sigma_\ell}\right) \phi\left(\frac{x_i - \mu_1}{\sigma_\ell}\right), \quad (54)$$

where  $\phi(x)$  is the normal distribution function given by

$$\phi(x) = \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{x^2}{2}\right), \quad (55)$$

with

$$\sigma_\ell = \sqrt{\gamma_{1,1}}. \quad (56)$$

This implies that the distribution of the voltage variable  $x_i(t)$  is described by the Gaussian distribution with the mean of  $\mu_1(t)$  and the variance of  $\gamma_{1,1}(t)$ . The probability given by Eq. (54) depends on the time because of the time dependence of  $x_i(t)$  and  $\sigma_\ell(t)$ . The probability  $W_{oi}(t)$  when  $x_i(t)$  at  $t$  is above the threshold  $\theta$  is given by [45]

$$W_{oi}(t) = 1 - \psi\left(\frac{\theta - \mu_1}{\sigma_\ell}\right), \quad (57)$$

where  $\psi(y)$  is the error function given by integrating  $\phi(x)$  from  $-\infty$  to  $y$ . Then the probability averaged over the ensemble is given by

$$\begin{aligned} W_\ell(t) &= \frac{1}{N} \sum_i W_{oi}(t), \\ &= 1 - \psi\left(\frac{\theta - \mu_1}{\sigma_\ell}\right). \end{aligned} \quad (58)$$

The fraction of a given neuron  $i$  emitting output spikes at  $t$  is given by

$$Z_\ell(t) = \frac{dW_o(t)}{dt} \Theta(\mu_1) = \phi\left(\frac{\theta - \mu_1}{\sigma_\ell}\right) \frac{d}{dt}\left(\frac{\mu_1}{\sigma_\ell}\right) \Theta(\mu_1). \quad (59)$$

where  $\dot{\mu}_1 = d\mu_1/dt$ . When we expand  $\mu_1(t)$  in Eq. (59) around  $t_o^*$  where  $\mu_1(t_o^*) = \theta$ , it becomes

$$Z_\ell(t) \sim \phi\left(\frac{t - t_o^*}{\delta t_{o\ell}}\right) \frac{d}{dt}\left(\frac{\mu_1}{\sigma_\ell}\right) \Theta(\dot{\mu}_1), \quad (60)$$

with

$$\delta t_{o\ell} = \frac{\sigma_\ell}{\dot{\mu}_1}, \quad (61)$$

where  $\mu_1$ ,  $\dot{\mu}_1$  and  $\sigma_\ell$  are evaluated at  $t = t_o^*$ .  $Z_\ell(t)$  provides the distribution of firing times, showing that most of firing times of neurons locate in the range given as

$$t_o \in [t_o^* - \delta t_{o\ell}, t_o^* + \delta t_{o\ell}]. \quad (62)$$

In the limit of vanishing  $\beta$ , Eq. (60) reduces to

$$Z_\ell(t) = \delta(t - t_o^*). \quad (63)$$

Similarly, we get the distribution for the global variable  $X$  given by (for details see Appendix D)

$$P(X) \simeq \left(\frac{1}{\sigma_g}\right) \phi\left(\frac{X - \mu_1}{\sigma_g}\right), \quad (64)$$

with

$$\sigma_g = \sqrt{\rho_{1,1}}. \quad (65)$$

This implies that the distribution of global voltage variable  $X(t)$  is described by the Gaussian distribution with the mean of  $\mu_1(t)$  and the variance of  $\rho_{1,1}(t)$ . If we define the  $m$ th firing time relevant to the global variable  $X(t)$  as

$$t_{gm} = \{t \mid X(t) = \theta; \dot{X}(t) > 0; t \geq t_{gm-1} + \tau_r\}, \quad (66)$$

the fraction of firing around  $t = t_o^*$  is given by

$$Z_g(t) = \phi\left(\frac{t - t_o^*}{\delta t_{og}}\right) \frac{d}{dt}\left(\frac{\mu_1}{\sigma_g}\right) \Theta(\dot{\mu}_1), \quad (67)$$

with

$$\delta t_{og} = \frac{\sigma_g}{\dot{\mu}_1}. \quad (68)$$

Then most of  $t_{og}$  locate in the range given by

$$t_g \in [t_o^* - \delta t_{og}, t_o^* + \delta t_{og}]. \quad (69)$$

Since  $\rho_{1,1}$  is generally smaller than  $\gamma_{1,1}$ , we get  $\sigma_g \leq \sigma_\ell$  and  $\delta t_{og} \leq \delta t_{o\ell}$ . In particular, in the case of no couplings, Eqs. (52), (56), (61), (65) and (68) lead to

$$\delta t_{og} = \frac{\delta t_{o\ell}}{\sqrt{N}}. \quad (\text{for } w = 0) \quad (70)$$

### Synchronous Response

Now we consider the quantity given by

$$R(t) = \frac{1}{N^2} \sum_{ij} \langle [x_i(t) - x_j(t)]^2 \rangle = 2(\gamma_{1,1} - \rho_{1,1}). \quad (71)$$

When all neurons are in the completely synchronous state, we get  $x_i(t) = X(t)$  for all  $i$ , and then  $R(t) = 0$ . On the contrary, in the asynchronous (random) state, we get  $R(t) = 2(1 - 1/N)\gamma_{1,1} \equiv R_0(t)$ . Then the quantity defined by

$$S(t) = 1 - R(t)/R_0(t) = \frac{(\rho_{1,1}/\gamma_{1,1} - 1/N)}{(1 - 1/N)}, \quad (72)$$

is 1 for the completely synchronous state and 0 for the asynchronous state. We hereafter call  $S(t)$  the *synchronization ratio*, which provides the degree of synchronous firings in the ensemble. We get  $S = 0$  for  $\beta \neq 0$  with no couplings ( $w = 0$ ), and  $S = 1$  for  $w \neq 0$  with no noises ( $\beta = 0$ ).

### D. Calculated results

We expect that our DMF equations given by Eqs. (20)-(27) may show bifurcation, synchronous and asynchronous states as well as chaotic states. In this study, we pay our attention to the response of the FN neuron ensembles to a single spike input,  $I^{(e)}(t)$  given by Eq. (4), which is applied to all neurons in the ensemble. We have adopted the parameters of  $\theta = 0.5$ ,  $\alpha = 0.1$ ,  $\tau_r = 10$ ,  $A = 0.10$ ,  $t_{in} = 100$  and  $T_w = 10$ . Parameter values of  $w$ ,  $\beta$  and  $N$  will be explained shortly. We get the critical magnitude of  $A_c = 0.0442$  below which firings of neuron defined by Eq. (53) cannot take place without noises ( $\beta = 0$ ). We have adopted the value of  $A = 0.10$  ( $> A_c$ ) for a study of the response to a supra-threshold input, related discussion being given in Sec. IV.

DMF calculations have been made by solving Eqs. (20)-(27) by the forth-order Runge-Kutta method with a time step of 0.01. Direct simulations have been performed by solving  $2N$  differential equations as given by Eqs. (1) and (2) by using also the forth-order Runge-Kutta method with a time step of 0.01. Simulation results are the average of 100 trials otherwise noticed. Initial values of variables are set to be  $\mu_1 = \mu_2 = \gamma_{1,1} = \gamma_{1,1} = \gamma_{1,2} = \rho_{1,1} = \rho_{2,2} = \rho_{1,2} = 0$  in DMF calculations, and  $x_i = y_i = 0$  for  $i = 1$  to  $N$  in direct simulations. All calculated quantities are dimensionless.

The time courses of means of  $\mu_1$  and  $\mu_2$  calculated with  $\beta = 0.01$ ,  $w = 0.0$  and  $N = 100$  are shown in Figs. 1(a) and 1(b), respectively, where solid curves denote the results of DMF

theory and dashed curves those of direct simulations. We note that  $\mu_1$  and  $\mu_2$  obtained by two methods are in very good agreement and they are indistinguishable. At the bottom of Fig. 1(a) an input spike is plotted [see also Fig. 2(a)]. States of neurons in an ensemble when an input spike is injected at  $t = 100$ , are randomized because noises have been already added since  $t = 0$ . Figures 1(c)-1(h) show the time courses of various variances and covariances. Agreements between the two methods are good for  $\gamma_{1,1}$ ,  $\rho_{1,1}$ ,  $\gamma_{1,2}$  and  $\rho_{1,2}$ . There is a fairly good agreement for  $\gamma_{2,2}$  and  $\rho_{2,2}$ . Comparing Figs. 1(c), 1(e) and 1(g) to 1(d), 1(f) and 1(h), respectively, we note that the relation given by Eq. (52):  $\rho_{\kappa,\lambda} = \gamma_{\kappa,\lambda}/100$  valid for  $w = 0$ , is supported by simulations: note that results in Figs. 1(d), 1(f) and 1(h) are multiplied by a factor of hundred.

Figures 2(a) shows a single spike input, which is applied at  $t = 100$  with a duration of  $T_w = 10$ . The solid curve in Fig. 2(b) express  $Z_\ell$ , the firing probability of the local variable  $x_i(t)$ , which is a positive derivative of  $W_\ell$  shown by the dashed curve [Eqs. (58) and (59)]. They are calculated for  $\beta = 0.01$ ,  $w = 0.0$  and  $N = 100$  in DMF theory. For a comparison, the simulation result for  $Z_\ell$  is plotted in Fig. 2(c). Firings of neurons occur at  $t_o \sim 104$  to  $105$  with a delay of about  $4 \sim 5$ . Fluctuations of firing times of local variables  $\delta t_{ol}$  are  $0.37$  calculated by Eq. (61) in DMF theory, and  $0.41$  in simulations which is the root-mean-square (RMS) value of firing times defined by Eq. (53). In contrast, dashed and solid curves in Fig. 2(d) show  $W_g$  and  $Z_g$ , respectively, for the global variable  $X(t)$  in DMF theory, while Fig. 2(e) shows  $Z_g$  obtained in simulations. Fluctuations in spike timings of the global variable are  $\delta t_{og} = 0.037$  calculated by Eq. (68) in DMF theory, and  $0.041$  in simulations which is the RMS value of firing times defined by Eq. (66). These figures of  $\delta t_{og}$  for the global variable are ten times smaller than respective values of  $\delta t_{ol}$  for the local variable.

### Noise-strength ( $\beta$ ) dependence

We expect that as the noise strength is more increased, the distribution of membrane potentials is more widen and fluctuations of firing times are more increased. Filled squares in Fig. 3(a) show the  $\beta$  dependence of  $\delta t_{ol}$  obtained by DMF theory [Eq. (61)] with  $w = 0.0$  and  $N = 100$ , while open squares express the RMS value of firing times obtained by simulations. The agreement between the two methods is fairly good. In contrast, filled circles in Fig. 3(a) show the  $\beta$  dependence of  $\delta t_{og}$  relevant to the global variable obtained by DMF theory [Eq. (68)] and open circles stand for RMS values of firing times in simulations. We note that  $\delta t_{og}$  is much smaller than  $\delta t_{ol}$  although both  $\delta t_{og}$  and  $\delta t_{ol}$  are proportional to  $\beta$  for weak noises under consideration. Figure 3(b) will be explained shortly in connection to the result of the  $w$  dependence.

### Cluster-size ( $N$ ) dependence

Filled squares in Fig. 4(a) show the  $N$  dependence of the local fluctuation of  $\delta t_{ol}$  for  $\beta = 0.01$  and  $w = 0.0$ , obtained by DMF theory, while open squares express that obtained by simulations. Simulations have not been performed for  $N > 100$  because of a limitation in our computer facility. We note that  $\delta t_{ol}$  is independent of  $N$  because of no couplings ( $w = 0$ ). In contrast, filled circles in Fig. 4(a) show the  $N$  dependence of the global fluctuation of  $\delta t_{og}$  obtained by DMF theory while open circles that by simulations. The relation:  $\delta t_{og} \propto (1/\sqrt{N})$ , holds as given by Eq. (70). Figure 4(b) for finite  $w$  will be

discussed shortly.

### Coupling-strength ( $w$ ) dependence

So far we have neglected coupling  $w$  among neurons, which is now introduced. Filled squares in Fig. 3(b) show the  $\beta$  dependence of local fluctuations of  $\delta t_{ol}$  calculated by DMF theory for  $w = 0.2$  and  $N = 100$ , while open squares that obtained by simulations. Filled and open circles express global fluctuations of  $\delta t_{og}$  in the DMF theory and simulations, respectively. Comparing these results with those for  $w = 0.0$  shown in Fig. 3(a), we note that  $\delta t_{ol}$  is much reduced as  $w$  is increased although there is little change in  $\delta t_{og}$ .

This is more clearly seen in Fig. 5(a), which shows the  $w$  dependence of firing-time fluctuations. Filled squares in Fig. 5(a) show fluctuations of  $\delta t_{ol}$  for the local variable obtained for  $\beta = 0.01$  and  $N = 100$  by the DMF theory while open squares express those calculated by simulations. Filled and open circles in Fig. 5(a) show fluctuations of  $\delta t_{og}$  for the global variable obtained by the DMF theory and simulations, respectively. When  $w$  is increased,  $\delta t_{ol}$  is considerably decreased whereas  $\delta t_{og}$  is almost constant. Figure 5(b) shows a similar plot of the  $w$  dependence of firing times when the size of an ensemble is reduced to  $N = 10$ . We note that  $\delta t_{og}$  for  $N = 10$  is 3.16 times larger than  $\delta t_{og}$  for  $N = 100$  because  $\delta t_{og}$  is proportional to  $1/\sqrt{N}$ .

Results obtained by DMF theory are analyzed in the Appendix E, where we get the expression for the  $w$ - and  $N$ -dependent  $\delta t_{ol}$  given by [see Eq. (E1)]

$$\frac{\delta t_{ol}(w, N)}{\delta t_{ol}(0, 1)} \sim 1 - \left(\frac{1}{2}\right)\left(1 - \frac{1}{N}\right)^n (a_1 w + a_2 w^2 + \dots), \quad (73)$$

where  $n = 1$ ,  $\delta t_{ol}(0, 1) = 2.71$ ,  $a_1 = 7.0$  and  $a_2 = -11.0$ . Bold, dashed curves for  $w \leq 0.2$  in Figs. 5(a) and 5(b) show the  $w$  dependence of  $\delta t_{ol}$  for  $N = 100$  and 10, respectively, expressed by Eq. (73), which are in good agreement with results of DMF theory shown by filled squares.

Log-log plots of Fig. 4(b) show the  $N$  dependence of  $\delta t_{ol}$  (squares) and  $\delta t_{og}$  (circles) for  $w = 0.2$  and  $N = 100$ , filled and open symbols denoting results of DMF and simulations, respectively. Although  $\delta t_{og} \propto (1/\sqrt{N})$  as in the case of  $w = 0$  [Fig. 4(a)],  $\delta t_{ol}$  shows the peculiar  $N$  dependence, which arises from the  $(1 - 1/N)$  term in Eq. (73). The  $N$  dependence given by Eq. (73) with  $n = 1$  and 2 is shown by thin solid curves at the uppermost in Fig. 4(b). The result with  $n = 1$  is in better agreement with the result of DMF theory shown by small filled squares than that with  $n = 2$  (see Appendix E).

Couplings among neurons work to increase the synchronous dynamics and to suppress local fluctuations. Figures 6(a) and 6(b) show the time sequence of the synchronization ratio  $S(t)$  defined by Eq. (72) for  $w = 0.1$  and  $w = 0.2$ , respectively, with  $\beta = 0.01$  and  $N = 100$ . Solid and dashed curves in Figs. 6(a) and 6(b) show results in DMF theory and simulations, respectively. Both results are in fairly good agreement. We note that  $S(t)$  has two peaks at times when  $\rho_{1,1}(t)$  also has double peaks [Fig.1(d)]. The maximum value of  $S(t)$  for  $w = 0.2$  is  $S_{\max} = 0.132$ , which is larger than  $S_{\max} = 0.041$  for  $w = 0.1$ . This trend is more clearly seen in Fig. 7 where the maximum magnitude of  $S(t)$ ,  $S_{\max}$ , is plotted as a function of  $w$  for  $N = 10, 20, 50$  and 100. It is shown that  $S_{\max}$  is increased as the coupling strength is increased, as expected. Figure 7 also shows that the effect of coupling is more significant in ensembles with smaller  $N$ .

An analysis of the result obtained in DMF theory yields the expression for  $w$ - and  $N$ -dependent  $S_{max}$  given by [see Eq. (E8) in Appendix E]

$$S_{max}(w, N) = c_1 w + c_2 w^2 + \dots, \quad (74)$$

with

$$c_1 = \left(\frac{1}{N}\right)\left(1 - \frac{1}{N}\right) b_1, \quad (75)$$

$$c_2 = \left(\frac{1}{N}\right)\left(1 - \frac{1}{N}\right) [b_2 + \left(1 - \frac{1}{N}\right)^2 b_1^2], \quad (76)$$

where  $b_1 = 22$  and  $b_2 = -290$ . Bold, dashed curves for  $w \leq 0.2$  in Fig. 7 show  $S_{max}$  expressed by Eqs. (74)-(76), which are in good agreement with results obtained in DMF theory shown by solid curves. If we define the coupling constant  $w_m(N)$  for which  $S_{max}$  is, for example, 0.3 for a given  $N$ , we get  $w_m(N) = 0.101, 0.147, 0.237$  and  $0.322$  for  $N = 10, 20, 50$  and  $100$ , respectively, which lead to  $w_m(N)/w_m(10) = 1.0, 1.46, 2.35$  and  $3.19$ , respectively, when  $w_m(N)$  is normalized by  $w_m(N = 10)$ . This suggests that we may get  $w_m(N) \propto \sqrt{N}$ . This arises from the fact that the relation:  $S_{max} \propto w^2/N$  is nearly hold for  $S_{max} = 0.3$  for which the contribution from the  $w^2$  term is more considerable than that from the  $w$  term in Eqs. (74)-(76). Of course, it is not the case for much smaller value of  $S_{max}$  for which the first term is more dominant than the second term.

Expressions of Eqs. (E1)-(E8) for  $w$ - and  $N$ -dependence of fluctuations and the synchronization ratio, which are obtained based on the results calculated in DMF theory, are useful in a phenomenological sense. For example, in the case of *negative* (inhibitory) couplings, Eqs. (E1) and (E8) yield an increase in  $\delta t_{ol}$  and a negative  $S$ , which are supported by numerical calculations with DMF theory and simulations (not shown). We have tried to extract coefficients  $a_1, a_2, b_1$  and  $b_2$  in Eqs. (E1)-(E8), by expanding Eqs. (20)-(29) in terms of  $w$ , but have not succeeded yet.

### III. LARGE CLUSTER CONSISTING OF MULTIPLE SUB-CLUSTERS

#### A. Formulation

It is possible to extend our DMF theory to a large FN neuron cluster which is divided into multiple  $M$  sub-clusters according to their functions. Dynamics of a single FN neuron  $i$  in a given sub-cluster  $m$  ( $=1$  to  $M$ ) which consists of  $N_m$  neurons, is described by the nonlinear DEs given by

$$\frac{dx_i(t)}{dt} = F[x_i(t)] - cy_i(t) + I_i^{(c1)}(t) + I_i^{(c2)}(t) + I_m^{(e)}(t) + \xi_i(t), \quad (77)$$

$$\frac{dy_i(t)}{dt} = bx_i(t) - dy_i(t) + e, \quad (i = 1 - N_m) \quad (78)$$

where  $x_i$  and  $y_i$  denote the fast (voltage) variable and slow (recovery) variable, respectively,  $\xi_i(t)$  the Gaussian white noise with  $\langle \xi_i(t) \rangle = 0$  and  $\langle \xi_i(t) \xi_j(t') \rangle = \beta_i^2 \delta_{ij} \delta(t - t')$ , the bracket  $\langle \cdot \rangle$  denoting the average [59]. In Eq. (77),  $I_i^{(c1)}(t)$  and  $I_i^{(c2)}(t)$  given by

$$I_i^{(c1)}(t) = (w_{mm}/N_m) \sum_{j \in m} G(x_j(t)), \quad (79)$$

$$I_i^{(c2)}(t) = \sum_{n(\neq m)} (w_{mn}/N_n) \sum_{k \in n} G(x_k(t)), \quad (80)$$

express the couplings within the sub-cluster  $m$  with the strength  $w_{mm}$ , and those between sub-clusters with the strength  $w_{mn}$ , respectively,  $N_m$  the number of neurons in the sub-cluster  $m$ , and  $G(x)$  is the sigmoid function.  $I_m^{(e)}(t)$  stands for an external single spike input applied to all neurons in the sub-cluster  $m$ , as given by Eq. (4).

As in the Sec. IIA, we first define the global variables for the sub-cluster  $m$  by

$$X^m(t) = (1/N_m) \sum_{i \in m} x_i(t), \quad (81)$$

$$Y^m(t) = (1/N_m) \sum_{i \in m} y_i(t), \quad (82)$$

and their averages by

$$\mu_1^m(t) = \langle X^m(t) \rangle, \quad (83)$$

$$\mu_2^m(t) = \langle Y^m(t) \rangle, \quad (84)$$

Next we define variances and covariances between intra-neuron variables, given by

$$\gamma_{1,1}^m = \frac{1}{N_m} \sum_{i \in m} \langle (\delta x_i^m)^2 \rangle, \quad (85)$$

$$\gamma_{2,2}^m = \frac{1}{N_m} \sum_{i \in m} \langle (\delta y_i^m)^2 \rangle, \quad (86)$$

$$\gamma_{1,2}^m = \frac{1}{N_m} \sum_{i \in m} \langle (\delta x_i^m \delta y_i^m) \rangle, \quad (87)$$

where  $\delta x_i^m = x_i(t) - \mu_1^m(t)$  and  $\delta y_i^m = y_i(t) - \mu_2^m(t)$ , and those between inter-neuron variables, given by

$$\rho_{1,1}^m = \langle (\delta X^m)^2 \rangle, \quad (88)$$

$$\rho_{2,2}^m = \langle (\delta Y^m)^2 \rangle, \quad (89)$$

$$\rho_{1,2}^m = \langle (\delta X^m \delta Y^m) \rangle, \quad (90)$$

where  $\delta X^m = X^m(t) - \mu_1^m(t)$  and  $\delta Y^m = Y^m(t) - \mu_2^m(t)$ . After some manipulations, we get the following differential equations:

$$\frac{d\mu_1^m}{dt} = f_0^m + f_2^m \gamma_{1,1}^m - c\mu_2^m + w_{mm} (1 - \frac{1}{N_m}) U_{0m} + \sum_{n(\neq m)} w_{mn} U_{0n} + I_m^{(e)}(t), \quad (91)$$

$$\frac{d\mu_2^m}{dt} = b\mu_1^m - d\mu_2^m + e, \quad (92)$$

$$\frac{d\gamma_{1,1}^m}{dt} = 2[(f_1^m + 3f_3^m \gamma_{1,1}^m) \gamma_{1,1}^m - c\gamma_{1,2}^m] + 2w_{mm} (\rho_{1,1}^m - \frac{\gamma_{1,1}^m}{N_m}) U_{1m}$$

$$+2 \sum_{n(\neq m)} w_{mn} \rho_{1,1}^n U_{1n} + \beta_m^2, \quad (93)$$

$$\frac{d\gamma_{2,2}^m}{dt} = 2(b\gamma_{1,2}^m - d\gamma_{2,2}^m), \quad (94)$$

$$\begin{aligned} \frac{d\gamma_{1,2}^m}{dt} &= b\gamma_{1,1}^m + (f_1^m + 3f_3^m\gamma_{1,1}^m - d)\gamma_{1,2}^m - c\gamma_{2,2}^m + w_{mm}(\rho_{1,2}^m - \frac{\gamma_{1,2}^m}{N_m}) U_{1m} \\ &+ \sum_{n(\neq m)} w_{mn} \rho_{1,2}^n U_{1n}, \end{aligned} \quad (95)$$

$$\frac{d\rho_{1,1}^m}{dt} = 2[(f_1^m + 3f_3^m\gamma_{1,1}^m)\rho_{1,1}^m - c\rho_{1,2}^m] + 2w_{mm} (1 - \frac{1}{N_m}) \rho_{1,1}^m U_{1m} + \frac{\beta_m^2}{N_m}, \quad (96)$$

$$\frac{d\rho_{2,2}^m}{dt} = 2(b\rho_{1,2}^m - d\rho_{2,2}^m), \quad (97)$$

$$\frac{d\rho_{1,2}^m}{dt} = b\rho_{1,1}^m + (f_1^m + 3f_3^m\gamma_{1,1}^m - d)\rho_{1,2}^m - c\rho_{2,2}^m + w_{mm} (1 - \frac{1}{N_m}) \rho_{1,2}^m U_{1m}, \quad (98)$$

with

$$U_{0m} = g_o^m + g_2^m \gamma_{1,1}^m, \quad (99)$$

$$U_{1m} = g_1^m + 3g_3^m \gamma_{1,1}^m, \quad (100)$$

where  $f_\ell^m = (1/\ell!)F^{(\ell)}(\mu_1^m)$ ,  $g_\ell^m = (1/\ell!)G^{(\ell)}(\mu_1^m)$ . and  $\beta_m^2 = \frac{1}{N_m} \sum_{i \in m} \beta_i^2$ . Now we have to solve  $8M$  dimensional deterministic differential equations, which is more amenable than to solve  $2NM$  stochastic DEs.

When a given cluster can be divided into excitatory and inhibitory sub-groups and when variance and covariance terms in Eqs. (91)-(98) are neglected, we get

$$\frac{d\mu_1^E}{dt} = f_0^E - c\mu_2^E + w_{EE} U_E + w_{EI} U_I + I_E^{(e)}(t), \quad (101)$$

$$\frac{d\mu_2^E}{dt} = b\mu_1^E - d\mu_2^E + e, \quad (102)$$

$$\frac{d\mu_1^I}{dt} = f_0^I - c\mu_2^I + w_{II} U_I + w_{IE} U_E + I_I^{(e)}(t), \quad (103)$$

$$\frac{d\mu_2^I}{dt} = b\mu_1^I - d\mu_2^I + e, \quad (104)$$

where the supra-script  $E$  and  $I$  stand for the excitatory and inhibitory clusters, respectively. This corresponds to the result of Wilson and Cowan [60]. Then our DMF theory given by Eqs. (91)-(98) may be regarded as a generalized version of the Wilson-Cowan theory including fluctuations of local and global variables.

### Firing-Time Distribution

The fraction of firings of neurons in the sub-cluster  $m$  is given by

$$Z_{om}(t) = \phi\left(\frac{\theta - \mu_1^m}{\sigma_{\ell m}}\right) \frac{d}{dt}\left(\frac{\mu_1^m}{\sigma_{\ell m}}\right) \Theta(\mu_1^m), \quad (105)$$

with



$$\sigma_{\ell m} = \sqrt{\gamma_{1,1}^m}. \quad (106)$$

When we expand  $\mu_1^m(t)$  in Eq. (105) around  $t_{om}^*$  where  $\mu_1^m(t_{om}^*) = \theta$ , it becomes

$$Z_{om}(t) \sim \phi\left(\frac{t - t_{om}^*}{\delta t_{om}}\right) \frac{d}{dt}\left(\frac{\mu_1^m}{\sigma_{\ell m}}\right) \Theta(\mu_1^m), \quad (107)$$

with

$$\delta t_{om} = \frac{\sigma_{\ell m}}{\dot{\mu}_1^m}, \quad (108)$$

where  $\mu_1^m$ ,  $\dot{\mu}_1^m$  and  $\sigma_{\ell m}$  are evaluated at  $t = t_{om}^*$ . This shows that most of firing times of a given sub-cluster  $m$  locate in the range given as

$$t_{om} \in [t_{om}^* - \delta t_{om}, t_{om}^* + \delta t_{om}]. \quad (109)$$

### Synchronous Response

The synchronization ratio of a given sub-cluster  $m$  is given by

$$S_m(t) = \frac{(\rho_{1,1}^m / \gamma_{1,1}^m - 1/N_m)}{(1 - 1/N_m)}, \quad (110)$$

which is 0 and 1 for completely asynchronous and synchronous states, respectively.

### B. Calculated results

We have performed model calculations, assuming  $M (= 10)$  sub-clusters, each of which consists of  $N_m (= N)$  neurons. They are connected by feed-forward inter-sub-cluster coupling given by  $w_{mn} = w_2 \delta_{nm-1}$ , which is allowed to be different from the intra-sub-cluster coupling given by  $w_{mm} = w_1$  for all  $m$ . A single spike input given by Eq. (4) is applied only to the first sub-cluster ( $m = 1$ ), and an output of a sub-cluster  $m$  is subsequently forwarded to the next sub-cluster  $m + 1$ . This is conceptually similar to the synfire chain [61]. When  $w_2$  is too small, signals cannot propagate through sub-clusters. The critical value of the inter-sub-cluster coupling  $w_{2c}$ , below which a spike cannot propagate through sub-clusters, is  $w_{2c} = 0.064, 0.028$  and  $0.020$  for  $w_1 = 0.0, 0.1$  and  $0.2$ , respectively, with  $\beta = 0.0$  and  $N = 100$ .

Figure 8(a) shows the time course of  $Z_{om}(t)$  calculated in DMF theory with  $\beta = 0.05$ ,  $w_1 = w_2 = 0.1$  and  $N = 100$ . Signals propagate through sub-clusters with  $\delta t_{om} \simeq 0.8$  for all  $m$ . The result is in good agreement with that obtained in direct simulations (not shown). Synchronization ratios  $S_m(t)$  shown in Fig. 8(b) have double peaks [see Figs. 6(a) and 6(b)]. The maximum value of  $S_m(t)$ , for example, is 0.022 for  $m = 1$  at  $t = 122.2$ .

In contrast, Fig. 8(c) shows the time course of  $Z_{om}(t)$  for the increased noise intensity of  $\beta = 0.23$ , which shows that signals cannot propagate, dying out at the sixth sub-cluster. In this case, the agreement of DMF results with simulations is not satisfactory. Synchronization ratios  $S_m(t)$  for  $\beta = 0.23$  shown in Fig. 8(d) have multiple peaks for  $1 \leq m \leq 4$ , double peaks for  $m = 5$ , a single peak for  $m = 6$ , and it disappears for  $m > 6$ .

Figure 9(a) shows the  $m$ -dependence of local fluctuations  $\delta t_{om}$  for various  $\beta$  with  $w_1 = w_2 = 0.1$  and  $N = 100$ . We note that  $\delta t_{om}$  is almost constant for  $\beta=0.05$  and  $0.10$ . In the case of  $\beta = 0.23$ , however,  $\delta t_{om}$  is divergently increased at  $m = 5$ . This behavior is not changed when we adopt a different set of parameters. Fig. 9(b) shows a similar plot of  $\delta t_{om}$  as a function of  $m$  for  $w_1 = 0.0$ ,  $w_2 = 0.1$  and  $N = 100$ . Signals propagate with  $\delta t_{om}=0.04$  and  $0.12$  for  $\beta=0.01$  and  $0.05$ , respectively. For  $\beta = 0.09$ , however, a spike dies out at  $m = 8$ .

Figure 10 shows the  $w_1$  dependence of the critical noise strength  $\beta_c$  above which signals cannot propagate. We get  $\beta_c = 0.09$  and  $0.23$  for  $w_1 = 0.0$  and  $0.1$ , respectively, for  $N = 100$  as discussed above. When  $w_1$  is set to be  $0.2$ ,  $\beta_c$  becomes  $0.38$  for  $N = 100$ . We note that  $\beta_c$  is almost linearly increased by increasing  $w_1$ . Figure 10 also shows that the critical value of  $\beta_c$  becomes larger as the size of sub-cluster ( $N$ ) is larger.

#### IV. CONCLUSION AND DISCUSSION

We have proposed DMF theory for stochastic FN neuron ensembles, in which means, variances and covariances of *local* and *global* variables are taken into account. DMF theory has been shown to be derived in various ways: series expansions of means, variances and covariances of local and global variables (Sec. IIA), re-arrangement of moments in RT's method (Sec. IIB) and a single-site approximation to RT's method [Sec. IIC] [56]. Our DMF theory, which assumes weak noises and the Gaussian distribution of state variables, goes beyond the weak coupling because no constraints are imposed on the coupling strength. Calculated results based on DMF theory are in fairly good agreement with those obtained by direct simulations for weak noises. When the noise intensity becomes stronger, the state-variable distribution more deviates from the Gaussian form (see Fig. 3 of [47]), and the agreement of results of DMF theory with those of simulations becomes worse. Nevertheless, our DMF theory is expected to be meaningful for qualitative or semi-quantitative discussion on the properties of neuron ensembles or clusters. It is possible to regard nonlinear differential equations given by Eqs. (20)-(27) [or Eqs. (91)-(98)] as the *mean-field FN model* for neuron ensembles or clusters. We hope that our DMF theory may play a role of the molecular-field (Weiss) theory in magnetism [57]: the Weiss theory provides a clear physical picture on various magnetic properties despite some disadvantages such that it yields too-high critical (Curie) temperature, wrong critical indices and wrong temperature dependence for magnetization at low temperatures. Our DMF theory may be applied to a general conductance-based nonlinear systems. When it is applied to an ensemble of  $N$  HH neurons, we get the  $24$  deterministic nonlinear differential equations, which are more amenable than original  $4N$  stochastic equations. Furthermore our DMF theory based on means, variances and covarinces of local and global variables can be applied to more general stochastic systems besides neural networks.

In summary, we have developed a semi-analytical DMF theory for FN neuron ensembles. In order to show the feasibility of the DMF theory, we have studied the response of ensembles of FN neurons to a single spike input. The result is summarized as follows: (i) the spike timing precision of the global variable is much improved by increasing the ensemble size, even when there is no couplings among constituent neurons, (ii) by increasing the coupling strength, the spike transmission is enhanced by the synchronous response, and (iii) the

spike propagation with a fairly precise timing is possible in large-scale clusters when the noise strength is moderate. The origin of the item (i) is the same as that yielding the central-limit theorem. Couplings work to suppress local fluctuations and to increase the synchronization ratio [Eq. (72)]. Items (i) and (ii) are consistent with the results reported previously [30]- [35]. The item (iii) agrees with the result of recent simulations for synfire chains, each layer of which consists of 100 IF neurons [62]. Items (i)-(iii) are beneficial to the population temporal-code hypothesis mentioned in the introduction. Although calculations reported in this paper have been limited to supra-threshold inputs, it is possible to study the response to sub-threshold inputs with the use of DMF theory. We may investigate combined effects of white noises and the heterogeneity in model parameters, which have been intensively studied in recent years [63]. Such calculations are in progress and will be reported in a separate paper.

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### APPENDIX A: DERIVATION OF EQS. (20)-(27) AND EQS. (32)-(36)

From Eqs. (9)-(12), we get the differential equations for the deviations of  $\delta x_i$  and  $\delta y_i$  of the neuron  $i$ , given by

$$\frac{d\delta x_i}{dt} = f_1\delta x_i + f_2(\delta x_i^2 - \gamma_{1,1}) + f_3\delta x_i^3 - c\delta y_i + \xi_i + \delta I_i^{(c)}, \quad (\text{A1})$$

$$\frac{d\delta y_i}{dt} = b\delta x_i - d\delta y_i, \quad (\text{A2})$$

with

$$\delta I_i^{(c)} = w \left( \frac{g_1}{N} \sum_{j(\neq i)} \delta x_j + g_2 \left[ \frac{1}{N} \sum_{j(\neq i)} \delta x_j^2 - \left(1 - \frac{1}{N}\right) \gamma_{1,1} \right] + \frac{g_3}{N} \sum_{j(\neq i)} \delta x_j^3 \right), \quad (\text{A3})$$

The differential equations for the variances and covariances are given by

$$\begin{aligned} \frac{d\gamma_{\kappa,\lambda}}{dt} &= \frac{d}{dt} \frac{1}{N} \sum_i < [(\delta x_i^2) \delta_{\kappa 1} \delta_{\lambda 1} + (\delta x_i \delta y_i) \delta_{\kappa 1} \delta_{\lambda 2} + (\delta y_i^2) \delta_{\kappa 2} \delta_{\lambda 2}] >, \\ &= \frac{1}{N} \sum_i < \{ 2[\delta x_i (\frac{d\delta x_i}{dt})] \delta_{\kappa 1} \delta_{\lambda 1} + [\delta y_i (\frac{d\delta x_i}{dt}) + \delta x_i (\frac{d\delta y_i}{dt})] \delta_{\kappa 1} \delta_{\lambda 2} \\ &\quad + 2[\delta y_i (\frac{d\delta y_i}{dt})] \delta_{\kappa 2} \delta_{\lambda 2} \} >, \end{aligned} \quad (\text{A4})$$

$$\frac{d\rho_{\kappa,\lambda}}{dt} = \frac{d}{dt} (1/N^2) \sum_i \sum_j < [(\delta x_i \delta x_j) \delta_{\kappa 1} \delta_{\lambda 1} + (\delta x_i \delta y_j) \delta_{\kappa 1} \delta_{\lambda 2} + (\delta y_i \delta y_j) \delta_{\kappa 2} \delta_{\lambda 2}] >$$

$$\begin{aligned}
&= \frac{1}{N^2} \sum_i \sum_j < \{ 2[\delta x_i (\frac{d\delta x_j}{dt})] \delta_{\kappa 1} \delta_{\lambda 1} + [\delta y_i (\frac{d\delta x_j}{dt}) + \delta x_i (\frac{d\delta y_j}{dt})] \delta_{\kappa 1} \delta_{\lambda 2} \\
&+ 2[\delta y_i (\frac{d\delta y_j}{dt})] \delta_{\kappa 2} \delta_{\lambda 2} \} >, \tag{A5}
\end{aligned}$$

In the process of the calculation using Eqs. (20)-(27), we have adopted the following approximations:

(1) the forth-order variances are assumed to be [47]

$$\frac{1}{N} \sum_i < \delta x_4 > = 3 \gamma_{1,1} \gamma_{1,1}, \tag{A6}$$

$$\frac{1}{N} \sum_i < \delta x_3 \delta y_i > = 3 \gamma_{1,1} \gamma_{1,2}, \tag{A7}$$

and

$$\frac{1}{N^2} \sum_i \sum_j < \delta x_i \delta x_j^3 > = 3 \gamma_{1,1} \rho_{1,1}, \tag{A8}$$

$$\frac{1}{N^2} \sum_i \sum_j < \delta y_i \delta x_j^3 > = 3 \gamma_{1,1} \rho_{1,2}, \tag{A9}$$

other forth terms being set zero.

(2) the third-order variances and terms higher than forth order are neglected,

Calculations of Eqs. (32)-(36) are similar to those discussed above if we read as  $m_1^i \rightarrow \mu_1$ ,  $m_2^i \rightarrow \mu_2$ ,  $\Delta x_i \rightarrow \delta x_i$  and  $\Delta y_i \rightarrow \delta y_i$ .

## APPENDIX B: SOME LIMITING CASES OF EQS. (20)-(27)

(1) In the limit of a single ( $N = 1$ ) neuron, Eqs. (20)-(27) reduce to

$$\frac{d\mu_1}{dt} = f_0 + f_2 \gamma_{1,1} - c\mu_1 + I^{(e)}(t), \tag{B1}$$

$$\frac{d\mu_2}{dt} = b\mu_1 - d\mu_2 + e, \tag{B2}$$

$$\frac{d\gamma_{1,1}}{dt} = 2(f_1 \gamma_{1,1} + 3f_3 \gamma_{1,1}^2 - c\gamma_{1,2}) + \beta^2, \tag{B3}$$

$$\frac{d\gamma_{2,2}}{dt} = 2(b\gamma_{1,2} - d\gamma_{2,2}), \tag{B4}$$

$$\frac{d\gamma_{1,2}}{dt} = b\gamma_{1,1} + (f_1 - d)\gamma_{1,2} + 3f_3 \gamma_{1,1} \gamma_{1,2} - c\gamma_{2,2}, \tag{B5}$$

$$\rho_{\kappa,\lambda} = \gamma_{\kappa,\lambda}. \tag{B6}$$

Equations (B1)-(B5) agree with the results of Rodriguez and Tuckwell (RT) [44] and Tanabe and Pakdaman (TP) [47]. In RT, the forth terms which appear in the process of calculating  $d\gamma_{1,1}/dt$  and  $d\gamma_{1,2}/dt$  in Eqs. (B3) and (B5), are assumed to be zero, whereas in TP, they are assumed to be as given by Eqs. (A6) and (A7).

(2) In the limit of large  $N$ , where the exclusion of the self-couplings in Eq. (3) may be neglected, Eqs. (20)-(27) become

$$\frac{d\mu_1}{dt} = f_0 + f_2\gamma_{1,1} - c\mu_2 + w U_0 + I^{(e)}(t), \quad (\text{B7})$$

$$\frac{d\mu_2}{dt} = b\mu_1 - d\mu_2 + e, \quad (\text{B8})$$

$$\frac{d\gamma_{1,1}}{dt} = 2[(f_1 + 3f_3\gamma_{1,1})\gamma_{1,1} - c\gamma_{1,2}] + 2w\rho_{1,1} U_1 + \beta^2, \quad (\text{B9})$$

$$\frac{d\gamma_{2,2}}{dt} = 2(b\gamma_{1,2} - d\gamma_{2,2}), \quad (\text{B10})$$

$$\frac{d\gamma_{1,2}}{dt} = b\gamma_{1,1} + (f_1 + 3f_3\gamma_{1,1} - d)\gamma_{1,2} - c\gamma_{2,2} + w\rho_{1,2}U_1, \quad (\text{B11})$$

$$\frac{d\rho_{1,1}}{dt} = 2[(f_1 + 3f_3\gamma_{1,1})\rho_{1,1} - c\rho_{1,2}] + 2w\rho_{1,1}U_1 + \frac{\beta^2}{N}, \quad (\text{B12})$$

$$\frac{d\rho_{2,2}}{dt} = 2(b\rho_{1,2} - d\rho_{2,2}), \quad (\text{B13})$$

$$\frac{d\rho_{1,2}}{dt} = b\rho_{1,1} + (f_1 + 3f_3\gamma_{1,1} - d)\rho_{1,2} - c\rho_{2,2} + w\rho_{1,2} U_1, \quad (\text{B14})$$

where  $U_0 = g_0 + g_2\gamma_{1,1}$  and  $U_1 = g_1 + 3g_3\gamma_{1,1}$ .

### APPENDIX C: DERIVATION OF EQ. (54)

The distribution  $P(x_i)$  in Eq. (54) is formally given by

$$P(x_i) = \int \dots \int \Pi_{j(\neq i)} dx_j \Pi_j dy_j p(x_1, \dots, x_N, y_1, \dots, y_N), \quad (\text{C1})$$

with the probability distribution function (pdf) of  $p(x_1, \dots, x_N, y_1, \dots, y_N)$  for the  $2N$ -dimensional vector  $\mathbf{z} = (x_1, \dots, x_N, y_1, \dots, y_N)$ , given by

$$p(x_1, \dots, x_N, y_1, \dots, y_N) = \frac{1}{(2\pi)^N \sqrt{|\mathbf{V}|}} \exp\left[-\frac{1}{2}(\mathbf{z} - \boldsymbol{\mu})^t \mathbf{V}^{-1} (\mathbf{z} - \boldsymbol{\mu})\right], \quad (\text{C2})$$

where  $\boldsymbol{\mu}$  and  $\mathbf{V}$  express the mean vector and the variance-covariance matrix, respectively,

In the case of a single FN neuron ( $N = 1$ ), pdf is given by

$$p(x_1, y_1) = p_1(x_1, y_1) = \frac{1}{(2\pi)\sqrt{|\mathbf{V}|}} \exp\left[-\frac{1}{2}(\mathbf{z} - \boldsymbol{\mu})^t \mathbf{V}^{-1} (\mathbf{z} - \boldsymbol{\mu})\right], \quad (\text{C3})$$

with

$$\mathbf{z} = (x_1, y_1)^t, \quad (\text{C4})$$

$$\boldsymbol{\mu} = (\mu_1, \mu_2)^t, \quad (\text{C5})$$

$$\mathbf{V} = \begin{pmatrix} \gamma_{1,1} & \gamma_{1,2} \\ \gamma_{1,2} & \gamma_{2,2} \end{pmatrix}. \quad (\text{C6})$$

Substituting Eqs. (C3)-(C6) to Eq. (C1), we get

$$P(x_1) = \int dy_1 p(x_1, y_1) = \frac{1}{\sqrt{\gamma_{1,1}}} \phi\left(\frac{x_1 - \mu_1}{\sqrt{\gamma_{1,1}}}\right), \quad (\text{C7})$$

where  $\phi(x)$  denotes the normal distribution function:

$$\phi(x) = \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{x^2}{2}\right). \quad (\text{C8})$$

In the case of arbitrary  $N$  under consideration, the calculation of  $P(x_i)$  may be performed within DMF as follows. As mentioned in Sec. IIC, our DMF theory assumes the configuration in which a *single* neuron is embedded in an effective medium characterized by  $\mu_\kappa$ ,  $\gamma_{\kappa,\lambda}$  and  $\rho_{\kappa,\lambda}$  [Eqs. (49)-(51)]. Thus it is effectively the problem of a single neuron in the effective medium. Means ( $\mu_\kappa$ ), variances ( $\gamma_{\kappa,\lambda}$ ) and covariances ( $\rho_{\kappa,\lambda}$ ) of local variables are determined by Eqs. (20)-(24). Then the calculation of  $P(x_i)$  for  $N > 1$  is the same as that for  $N = 1$  mentioned above, and it is given by

$$P(x_i) = \int dy_1 p(x_1, y_1) = \frac{1}{\sqrt{\gamma_{1,1}}} \phi\left(\frac{x_i - \mu_1}{\sqrt{\gamma_{1,1}}}\right). \quad (\text{C9})$$

#### APPENDIX D: DERIVATION OF EQ. (64)

Equations (20), (21), (25)-(27) form DEs for means ( $\mu_\kappa$ ), variances ( $\gamma_{\kappa,\lambda}$ ) and covariances ( $\rho_{\kappa,\lambda}$ ) for global variables,  $X$  and  $Y$ . Then  $P(X)$  in Eq. (64) is given by

$$P(X) = \int dY p(X, Y), \quad (\text{D1})$$

with pdf for the two-dimensional vector  $\mathbf{z} = (X, Y)^t$  given by

$$p(X, Y) = \frac{1}{2\pi\sqrt{|\mathbf{V}|}} \exp\left[-\frac{1}{2}(\mathbf{z} - \boldsymbol{\mu})^t \mathbf{V}^{-1} (\mathbf{z} - \boldsymbol{\mu})\right], \quad (\text{D2})$$

with

$$\boldsymbol{\mu} = (\mu_1, \mu_2)^t, \quad (\text{D3})$$

$$\mathbf{V} = \begin{pmatrix} \rho_{1,1} & \rho_{1,2} \\ \rho_{1,2} & \rho_{2,2} \end{pmatrix}. \quad (\text{D4})$$

Substituting Eqs. (D2)-(D4) to Eq. (D1), we obtain

$$P(X) = \frac{1}{\sqrt{\rho_{1,1}}} \phi\left(\frac{X - \mu_1}{\sqrt{\rho_{1,1}}}\right), \quad (\text{D5})$$

where  $\phi(x)$  denotes the normal distribution [Eq. (C8)].

Alternatively  $P(X)$  is expressed by

$$P(X) = \int \dots \int \Pi_i dx_i \Pi_i dy_i p(x_1, \dots, x_N, y_1, \dots, y_N) \delta(X - \frac{1}{N} \sum_i x_i), \quad (\text{D6})$$

where  $p(x_1, \dots, x_N, y_1, \dots, y_N)$  stands for pdf for  $2N$ -dimensional vector [Eq. (C2)]. However, a calculation of  $P(X)$  based on Eq. (D6) is difficult except for the no coupling case ( $w = 0$ ), for which pdf is given by

$$p(x_1, \dots, x_N, y_1, \dots, y_N) = \Pi_j p_1(x_i, y_i), \quad (\text{D7})$$

$p_1(x_i)$  being pdf for  $N = 1$  [Eq. (C3)]. Performing integrals with respect to  $y_i$  in Eq. (D6) with Eq. (D7), we get

$$P(X) = \int \dots \int \Pi_i dx_i \Pi_i \frac{1}{\sqrt{\gamma_{1,1}}} \phi\left(\frac{x_i - \mu_1}{\sqrt{\gamma_{1,1}}}\right) \delta(X - \frac{1}{N} \sum_i x_i), \quad (\text{D8})$$

By using the procedure conventionally used for proofing the central-limit theorem, we obtain Eq. (D5) with  $\rho_{1,1} = \gamma_{1,1}/\sqrt{N}$  (for  $w = 0$ ). We should note that, a calculation of  $P(X)$  based on Eq. (D1) is easier than that based on Eq. (D6) and that the former is applicable for finite couplings.

## APPENDIX E: ANALYSIS OF NOISE, COUPLING AND SIZE DEPENDENCE

### (1) $\delta t_{ol}$ and $\delta t_{og}$

Based on the calculated results of DMF theory, we have tried to obtain the analytical expression of  $\beta$ -,  $w$ - and  $N$ -dependence of  $\delta t_{ol}$  and  $\delta t_{og}$ . Figures 3(a) and 3(b) show that  $\delta t_{ol}$  and  $\delta t_{og}$  are proportional to  $\beta$  for weak noises, for which both  $\gamma_{1,1}$  and  $\rho_{1,1}$  are proportional to  $\beta^2$  [see Eqs. (56), (61), (65) and (68)]. From results shown in Figs. 4 and 5, we have obtained expressions given by

$$\frac{\delta t_{ol}(w, N)}{\delta t_{ol}(0, 1)} \sim 1 - \left(\frac{1}{2}\right)\left(1 - \frac{1}{N}\right)^n (a_1 w + a_2 w^2 + \dots), \quad (\text{E1})$$

$$\frac{\delta t_{og}(w, N)}{\delta t_{ol}(0, 1)} \sim \frac{1}{\sqrt{N}}, \quad (\text{E2})$$

where  $n = 1$ ,  $\delta t_{ol}(0, 1) = 2.71$ ,  $a_1 = 7.0$  and  $a_2 = -11.0$ . The  $N$  dependence of  $\delta t_{ol}$  expressed by Eq. (E1) with  $n = 1$  and 2 are shown by thin solid curves at the uppermost in Fig. 4(b) with DMF result (small filled squares): these results are shifted upward by 0.433 for a clarity of the figure. The result with  $n = 1$  is in better agreement with the DMF result than that with  $n = 2$ . On the other hand, bold, dashed curves in Fig. 5(a) and 5(b) show the  $w$  dependence of  $\delta t_{ol}$  for  $N = 100$  and 10, respectively, expressed by Eq. (E1) with  $n = 1$ , which is in good agreement with results of DMF theory shown by filled squares. This implies from Eqs. (56), (61), (65) and (68) that the  $w$ - and  $N$ -dependence of  $\gamma_{1,1}$  and  $\rho_{1,1}$  evaluated at  $t = t_o^*$  where  $\mu_1(t_o^*) = \theta$ , are given by

$$\frac{\gamma_{1,1}(w, N)}{\gamma_{1,1}(0, 1)} \sim 1 - (1 - \frac{1}{N}) (a_1 w + a_2 w^2 + \dots), \quad (\text{E3})$$

$$\frac{\rho_{1,1}(w, N)}{\gamma_{1,1}(0, 1)} \sim \frac{1}{N}. \quad (\text{E4})$$

Note that  $\delta t_{ol}(0, 1)$  and  $\gamma_{1,1}(0, 1)$  are proportional to  $\beta$  and  $\beta^2$ , respectively.

(2)  $S_{max}$

In order to discuss the expression of  $\beta$ -,  $w$ - and  $N$ -dependent  $S_{max}$ , we have analyzed results of  $S_{max}$  shown in Fig. 7 by

$$S_{max} = c_1 w + c_2 w^2 + \dots, \quad (\text{E5})$$

to guess how expansion coefficients of  $c_1$  and  $c_2$  depend on  $N$ . After several tries, we have concluded that the  $w$ - and  $N$ -dependence of  $\gamma_{1,1}$  and  $\rho_{1,1}$  evaluated at  $t = t_o^{(m)}$  where  $\rho_{1,1}(t)$  has the maximum value, may be given by

$$\frac{\gamma_{1,1}(w, N)}{\gamma_{1,1}(0, 1)} \sim 1 - (1 - \frac{1}{N})^m (b_1 w + b_2 w^2 + \dots), \quad (\text{E6})$$

$$\frac{\rho_{1,1}(w, N)}{\gamma_{1,1}(0, 1)} \sim \frac{1}{N}, \quad (\text{E7})$$

yielding  $S_{max}$  given by [see Eq. (72)]

$$S_{max}(w, N) = (\frac{1}{N})(1 - \frac{1}{N})^{m-1} \{b_1 w + [b_2 + (1 - \frac{1}{N})^2 b_1^2] w^2\}, \quad (\text{E8})$$

where  $m = 2$ ,  $b_1 = 22$  and  $b_2 = -290$ . Bold, dashed curves in Fig. 7 show the  $w$  dependence of  $S_{max}$  expressed by Eq. (E8) for various  $N$  values, which are in fairly good agreement with results of DMF theory shown by solid curves. We should point out that a factor of  $(1 - 1/N)$  in Eqs. (E1), (E3), (E6) and (E8) appears because the coupling  $w$  does not work in a single-neuron case ( $N = 1$ ) and that at least the second power ( $m = 2$ ) is necessary in Eq. (E6) for  $S_{max}$  to vanish in the  $N = 1$  limit. A functional form of Eq. (E3) may be different from that of Eq. (E6) because the former is evaluated at  $t_o^*$  while the latter at  $t_o^{(m)}$ . Our DMF calculation shows that when  $\beta$  is increased for a fixed (finite)  $w$  value,  $S_{max}$  is gradually decreased, although Eq. (E8) has no  $\beta$  dependence. This is due to contributions of  $O(\beta^4)$  to  $\gamma_{1,1}$  and  $\rho_{1,1}$ , which have been not included in the above discussion.



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## FIGURES

FIG. 1. Time courses of means, variances and covariances calculated by DMF theory (solid curves) and simulations (dashed curves): (a)  $\mu_1$ , (b)  $\mu_2$ , (c)  $\gamma_{1,1}$ , (d)  $\rho_{1,1}$ , (e)  $\gamma_{2,2}$ , (f)  $\rho_{2,2}$ , (g)  $\gamma_{1,2}$  and (h)  $\rho_{1,2}$ , for  $A = 0.10$ ,  $\beta = 0.01$ ,  $w = 0.0$  and  $N = 100$ . Results of (d), (f) and (h) are multiplied by a factor of hundred. The chain curve at the bottom of (a) expresses a single input spike,  $I^{(e)}$  in Eq. (4) [see also Fig. 2(a)].

FIG. 2. Time courses of (a)  $I^{(e)}$ , (b)  $W_\ell$  (the dashed curve) and  $Z_\ell$  (the solid curve) in DMF theory, (c)  $Z_\ell$  in simulations, (d)  $W_g$  (the dashed curve) and  $Z_g$  (the solid curve) in DMF theory, and (e)  $Z_g$  in simulations, for  $A = 0.10$ ,  $\beta = 0.01$ ,  $w = 0.0$  and  $N = 100$ .

FIG. 3. (a) The  $\beta$  dependence of  $\delta t_{ol}$  (squares), and  $\delta t_{og}$  (circles) for  $w = 0.0$  and (b) that for  $w = 0.2$  with  $N = 100$ , filled symbols denoting results in DMF theory and open symbols those in simulations.

FIG. 4. Log-log plots of  $\delta t_{ol}$  (squares) and  $\delta t_{og}$  (circles) against  $N$  for (a)  $w = 0.0$  and (b)  $w = 0.2$ , filled symbols denoting results in DMF theory and open symbols those in simulations. Shown at the uppermost in (b) are the DMF result (small, filled squares) and results with Eq. (E1) with  $n = 1$  and 2 (thin solid curves): they are shifted upward by 0.433 for a clarity of the figure (see text).

FIG. 5. The  $w$  dependence of  $\delta t_{ol}$  (squares) and  $\delta t_{og}$  (circles) for (a)  $N = 100$  and (b)  $N = 10$  with  $\beta = 0.01$ , filled symbols denoting results in DMF theory and open symbols those in simulations. Bold, dashed curves for  $w \leq 0.2$  express Eq. (73) (see text).

FIG. 6. The time course of synchronization ratio  $S$  for (a)  $w = 0.1$  and (b)  $w = 0.2$  with  $\beta = 0.01$  and  $N = 100$ , solid curve denoting results of DMF theory and dashed curve those of simulations.

FIG. 7. The  $w$  dependence of the maximum of  $S$ ,  $S_{max}$ , for  $N = 10$  (squares),  $N = 20$  (triangles),  $N = 50$  (inverted triangles) and  $N = 100$  (circles) with  $\beta = 0.01$ , filled symbols denoting results of DMF theory and open symbols those of simulation. Bold, dashed curves for  $w \leq 0.2$  express Eq. (74) (see text).

FIG. 8. Time courses of  $Z_{om}$  for (a)  $\beta = 0.05$  and (b)  $\beta = 0.23$  with  $w_1 = w_2 = 0.1$ , and time courses of  $S_m$  for (c)  $\beta = 0.05$  and (d)  $\beta = 0.23$  with  $w_1 = w_2 = 0.1$ , calculated for  $N = 100$  and  $M = 10$  by DMF theory.

FIG. 9.  $\delta t_{om}$  as a function of  $m$  for (a)  $w_1 = w_2 = 0.1$  and (b)  $w_1 = 0.1$  and  $w_2 = 0.0$  with  $N = 100$  and  $M = 10$ .

FIG. 10. The  $w_1$  dependence of  $\beta_c$  for various  $N$  values with  $w_2 = 0.1$ .

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This figure "fig6-10.gif" is available in "gif" format from:

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